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Developmental Genetic Analysis of Seed Size in Soybean (*Glycine max*)

LI Wen-Xia[1,2,3], NING Hai-Long[1,3,①], LI Wen-Bin[1,3,①], LÜ Wen-He[2]

1. *Soybean Research Institute, Northeast Agricultural University, Harbin* 150030, *China*;
2. *College of Agronomy, Northeast Agricultural University, Harbin* 150030, *China*;
3. *Key Laboratory of Soybean Biology of Education Ministry, Harbin* 150030, *China*

Abstract: Seed size is one of the important factors of soybean [*Glycine max* (L.) Merrill] yield. There have been lots of reports about genetic effects and physiology—ecological researches on seed size, but the genetic behaviors of genes during seeds development were rarely discussed. Analysis of main genetic effects for fresh seed size (FSS) and dry seed size (DSS) of soybean was conducted with diallel cross data by using a seed genetic model. Analyses of unconditional and conditional variances and correlations were used to evaluate the developmental behavior of soybean. The phenotypic means of FSS and DSS in soybean at eight stages among three generations reached the highest value at 9/6 and 9/13, respectively. The means of FSS decreased dramatically after 9/6, but the means of DSS maintained relatively stable tendency at corresponding periods. The unconditional variance analysis showed that FSS and DSS were controlled by embryo, cytoplasmic and maternal effects in the whole growth period. Genetic effects due to cytoplasmic and maternal effects were relatively important for FSS and DSS at most of the growth periods. Conditional variance analysis showed that genes from different genetic system expressed discontinuously in the whole growth period. The net genetic effects due to cytoplasmic and maternal plant on FSS and DSS were larger than those of embryo effects at most of the growth periods. Different genetic system can affect the relationship of various stages to mature solely or simultaneously. Embryo additive effects at 8/16, embryo dominance effects at 8/9 and 8/16, maternal plant dominance effects at 8/2 and 8/16 could ultimately affect the performance of FSS at maturing stage. Embryo additive effects at 8/2 and 9/13, cytoplasm effects at 8/9, maternal plant dominance effects at 8/2 could ultimately affect the performance of DSS.

Key words: developmental behavior; genetic effect; fresh seed size; dry seed size; soybean

Seed size is one of most important factors of soybean (*Glycine max* L.) yield. Up to now, there have been lots of reports about genetic analysis and ecological effects on seed size. Genetic effects, heritability, combining ability and correlation with other agronomic traits were predicted by corresponding mating design and established genetic models [1-10]. Soybean seed traits may be simultaneously controlled by nuclear genes, cytoplasm genes, and maternal nuclear genes [11-14]. Following the genetic models for analyzing embryo, cytoplasm, and maternal effects for diploid seeds proposed by Zhu [11, 13, 14], Ning *et al.* [15] found that the matured soybean seed size was controlled by embryo, cytoplasm, and maternal effects simultaneously. As regards ecological effects, the role of meteorological factors and some cultivated measures on soybean seed size was investigated [16-18]. There were a few descriptions on the developmental behavior of soybean seed size [19].

The development of soybean seed is not only an orderly expression process of seed genes, but also the dynamic procedure of substances accumulating in embryo. Recently, Zhu [20] developed a mixed model approach, by which conditional genetic effects and conditional variance components, such as embryo

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① Corresponding author. E-mail: ninghailong1975@163.com, wenbinli@yahoo.com; Tel: +86-451-5519 1042 additive $V_{A(t|t-1)}$, embryo dominance $V_{D(t|t-1)}$, cytoplasmic $V_{C(t|t-1)}$, maternal additive $V_{Am(t|t-1)}$, maternal dominance $V_{Dm(t|t-1)}$ were analyzed. The genetic effects at time *t* conditional on the causal genetic effects at time (*t*-1) could imply the new effects of genes that were independent of the causal genetic effects, and the new effects of genes were net genetic effects at the period from time (*t*-1) to time *t*. This method has been employed to study boll number and cotton seed yield [21] and some seed quality (oil index, protein index, lysine index) traits [22] in upland cotton, body weight, and tail length in mice [23], transparency and chalkiness area [24] and brown rice checkness [25] and weight [26] in rice and so on. But there were few reports about genetic analysis for developmental behavior of soybean seed size at various stages which would have been useful to profound understanding of the inheritance during soybean development. In the present research, this method was used to analyze the developmental genetics of soybean seed size. The objective of this article was to find new genetic theory for soybean breeding.

1 Materials and Methods

1. 1 Materials and field experiment

The data described in this article were derived from an incomplete diallel cross among five different spring soybean genotypes: Dongnong 42, Dongnong 46, Dongnong 7819, Nongda 5129, and Heinong 35 from Heilongjiang Province, which had the same growth period and could mature normally at Harbin. The mating experiment was conducted at Northeast Agriculture University (NEAU), Harbin, China in 2001. The F_1 seeds were planted in Hainan Province in the winter of 2002. Seeds of all the parents, F_1 and F_2, were sown in the field at NEAU in 2003. The field experiment was conducted using a randomized complete block design with three replicates. Each plot consisted of various rows of 5 m length and the two rows were 65 cm apart, in which plants were spaced by 10 cm. From the plants, which were tagged at flowering one-half at the same day (6/30) (month/day), 30–50 soybean pods were sampled from five nodes in the middle nodes of the main stem at weekly intervals from 8/2 to 9/20, and were designated S1(8/2), S2(8/9), S3(8/16), S4(8/23), S5(8/30), S6(9/6), S7(9/13), and S8(9/20). The fresh seeds were dried by Constant Temperature Torrefaction Box 101–3 (Shanghai Nanyang Instrument Co., Ltd., Shanghai, China). Fresh seed size (FSS) and dry seed size (DSS) were measured and were denoted as g/100 seeds.

1. 2 Statistical analysis

The genetic model of diploid seeds for quantitative traits of embryo, cytoplasmic, and maternal plant effects was employed to study the inheritance of seed size[11]. Unconditional variance components (embryo additive V_{Ao}, embryo dominance V_{Do}, cytoplasmic V_C, maternal additive V_{Am}, maternal dominance V_{Dm}) and conditional variance components (conditional embryo additive $V_{Ao(t|t-1)}$, conditional embryo dominance $V_{Do(t|t-1)}$, conditional cytoplasmic $V_{C(t|t-1)}$, conditional maternal additive $V_{Am(t|t-1)}$, conditional maternal dominance $V_{Dm(t|t-1)}$) were estimated by minimum norm and quadratic unbiased estimation (MINQUE) method [11, 27]. Unconditional correlation coefficients (phenotypic correlation coefficient r_p, embryo additive correlation coefficient r_{Ao}, embryo dominance correlation coefficient r_{Do}, cytoplasmic correlation coefficient r_C, maternal plant additive correlation coefficient r_{Am}, maternal plant dominance correlation coefficient r_{Dm}) and conditional correlation coefficients (conditional phenotypic correlation coefficient $r_{p(t|t-1)}$, conditional embryo additive correlation coefficient $r_{A(t|t-1)}$, conditional embryo dominance correlation coefficient $r_{D(t|t-1)}$, conditional cytoplasmic correlation coefficient $r_{C(t|t-1)}$, conditional maternal plant additive correlation coefficient $r_{Am(t|t-1)}$, conditional maternal plant dominance correlation coefficient $r_{Dm(t|t-1)}$) between various developmental stages were calculated. An adjusted unbiased prediction (AUP) method was employed to predict genetic effect [28]. Jackknifing was used to estimate standard errors of estimated genetic variances and correlation coefficients [11, 29]. The *t* test was applied to test the significance of genetic parameters.

2 Results

2. 1 Phenotypic means of generations

Means of FSS (fresh seed size) and DSS (dry seed size) in soybean at eight stages among three generations are presented in Fig. 1. Three generations reach the biggest value for FSS at S6, and for DSS at S7. Both FSS and DSS increased rapidly from S2 to S6. Means of FSS decreased dramatically after S6, but means of DSS remained stable at corresponding periods. For FSS, phenotypic means of F_2 seeds were higher than those of parents and F_1, except for the last two stages. But for DSS, means of F_2 generation were higher than those of parents and F_1 at almost all stages.

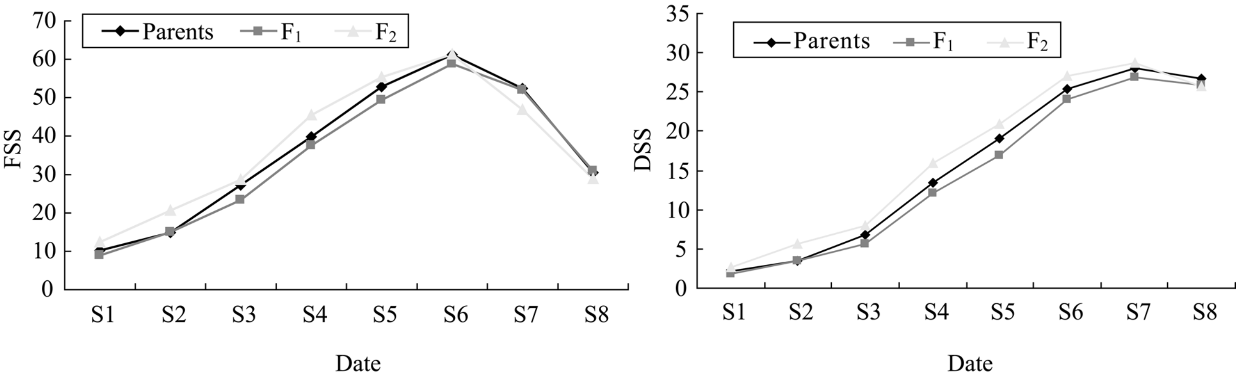

Fig. 1 Phenotypic means of FSS (fresh seed size) **and DSS** (dry seed size) **at eight developmental stages**

2. 2 Variance components

The variances associated with the various causal components for FSS and DSS are shown in Table 1.

Significant unconditional variance of embryo additive effects, embryo dominance effects, cytoplasmic effects, maternal additive effects and maternal dominance effects were noticeably detected at most stages for FSS and DSS. This suggested that FSS and DSS were controlled by embryo effects, cytoplasmic effects, and maternal effects in the whole growth period. The result also showed that gene effects from different genetic systems acted on the seed size solely or simultaneously. The sum of embryo effects ($V_{Ao}+V_{Do}$) were less than those of cytoplasmic and maternal effects ($V_C+V_{Am}+V_{Dm}$) with the exception of S3 and S7 for FSS and S3 and S5 for DSS, indicating that FSS and DSS were mainly controlled by cytoplasmic and maternal effects at most of the growth periods.

Conditional variance analysis showed that genes of different genetic system expressed discontinuously in the whole growth period. Net genetic effects from different system could affect the performance of FSS and DSS solely or simultaneously in various stages. The sum of conditional embryo variance ($V_{Ao(t|t-1)}+V_{Do(t|t-1)}$) was less than that of cytoplasmic and maternal effects ($V_{C(t|t-1)}+V_{Am(t|t-1)}+V_{Dm(t|t-1)}$) with the exception of S2 | S1, S3 | S2 and S8 | S7 for FSS, and S2 | S1 and S4 | S3 for DSS. This indicates that the net genetic effects of cytoplasmic and maternal plant on FSS and DSS were larger than those of embryo effects at most growth periods.

2. 3 Correlation coefficients

It would be useful to examine the genetic correlation for seed size traits at different stages (e.g., between S1 and S8 for FSS). This approach facilitates the understanding about (1) whether the same genes control the trait throughout the developmental stage; (2) whether the final expression of a trait could be predicted on the basis of the early phenotype; and (3) whether the genetic association pattern would be altered by various gene expression of each trait at specific time intervals.

Table 1 Estimation of unconditional and conditional variances of FSS (fresh seed size) **and DSS** (dry seed size) **at eight developmental stages**

	V_{Ao}	V_{Do}	V_C	V_{Am}	V_{Dm}
FSS					
S1	0.722**	0.000	2.182**	0.000	2.241**
S2	3.310**	1.003**	2.618**	0.000	8.131**
S3	12.175**	4.895**	0.000	1.207**	0.710**
S4	0.000	4.618**	35.947**	0.000	9.133**
S5	1.511**	1.628**	0.000	5.049**	0.000
S6	0.000	4.048**	0.000	0.000	6.718**
S7	6.639**	12.354**	12.747**	0.000	0.000
S8	0.887**	1.427**	0.760**	0.000	2.604**
S1 | initial	0.722**	0.000	2.182**	0.000	2.241**
S2 | S1	0.000	2.528**	0.938**	0.000	0.000
S3 | S2	3.695**	3.842**	0.000	1.702**	0.600**
S4 | S3	0.000	0.000	0.924**	0.930**	0.000
S5 | S4	0.000	0.000	0.000	37.500**	0.942**
S6 | S5	0.000	15.935**	26.378**	16.542**	0.000
S7 | S6	0.000	3.436**	80.269**	0.000	8.299**
S8 | S7	3.872**	1.281**	0.000	0.256**	2.946**
DSS					
S1	0.255**	0.000	0.236**	0.077**	0.005**
S2	0.389**	0.112**	0.111**	0.000	1.120**
S3	1.342**	0.000	0.504**	0.367**	0.217**
S4	0.000	1.246**	5.160**	0.000	3.474**
S5	0.000	1.521**	0.931**	0.169**	0.201**
S6	0.000	2.466**	0.000	0.000	4.735**
S7	1.135**	0.000	0.000	0.328**	2.203**
S8	0.805**	0.169**	1.736**	0.000	0.009**
S1 | initial	0.255**	0.000	0.236**	0.077**	0.005**
S2 | S1	0.000	0.388**	0.062**	0.000	0.000
S3 | S2	0.621**	0.000	0.000	0.762**	0.218**
S4 | S3	0.000	0.607**	0.000	0.464**	0.000
S5 | S4	1.341**	0.000	4.168**	0.767**	0.000
S6 | S5	0.000	0.638**	29.284**	10.164**	3.251**
S7 | S6	12.040**	0.000	8.182**	0.000	4.169**
S8 | S7	151.109**	0.000	172.077**	0.000	90.175**

** Significant at 0.01 level; V_{Ao} : embryo additive variance component; V_{Do} : embryo dominance variance component; V_C : cytoplasmic variance component; V_{Am} : maternal additive variance component; V_{Dm} : maternal dominance variance component.

2. 3. 1 FSS

The components of the genetic correlation for FSS with itself at various intervals are described in Tables 2 and 3. The unconditional and conditional phenotypic correlation coefficients between various stages and mature FSS were not significantly different from zero except for $r_{p(\mathrm{S5|S4})/(\mathrm{S8|S7})}$ and $r_{p(\mathrm{S6|S5})/(\mathrm{S8|S7})}$. This indicates that accumulated gene effects at various stages could not affect significantly the ultimate performance, and the net gene effects at S5 and S6 could ultimately reduce the mature FSS. As regards the correlation component analysis, different genetic systems could affect the relationship of various stages to mature solely or simultaneously. It was shown, by significantly positive unconditional $r_{Ao\mathrm{S3/S8}}$ and conditional $r_{Ao(\mathrm{S3|S2})/(\mathrm{S8|S7})}$, unconditional $r_{Do\mathrm{S2/S8}}$ and conditional $r_{Do(\mathrm{S2|S1})/(\mathrm{S8|S7})}$, significantly negative unconditional $r_{Do\mathrm{S3/S8}}$ and conditional $r_{Do(\mathrm{S3|S2})/(\mathrm{S8|S7})}$, unconditional $r_{Dm\mathrm{S1/S8}}$ and conditional $r_{Dm(\mathrm{S1|initial})/(\mathrm{S8|S7})}$, unconditional

Table 2 Estimates of unconditional correlation coefficients of FSS (fresh seed size) **at eight developmental stages**

Stage 1	Stage 2	r_p	r_{Ao}	r_{Do}	r_C	r_{Am}	r_{Dm}
S1	S2	0.240^{*}	0.169^{+}	0.000	0.115	0.000	0.018
	S3	0.230^{*}	0.398^{**}	0.000	0.000	0.000	0.034
	S4	0.305^{*}	0.000	0.000	0.331^{**}	0.000	-0.151^{+}
	S5	0.190^{+}	0.468^{**}	0.000	0.000	0.000	0.000
	S6	0.194	0.000	0.000	0.000	0.000	-0.224^{**}
	S7	-0.270^{**}	-0.447^{**}	0.000	-0.169^{*}	0.000	0.000
	S8	−0.055	0.143	0.000	-0.205^{*}	0.000	-0.159^{*}
S2	S3	0.257^{*}	0.275^{**}	0.041	0.000	0.000	0.084
	S4	0.299^{**}	0.000	0.112^{*}	0.646^{**}	0.000	-0.144^{+}
	S5	0.252^{**}	0.275^{**}	−0.091	0.000	0.000	0.000
	S6	0.063	0.000	0.381^{**}	0.000	0.000	-0.351^{**}
	S7	-0.274^{*}	−0.143	−0.100	-0.349^{**}	0.000	0.000
	S8	−0.131	0.533^{**}	0.266^{**}	-1.000^{**}	0.000	-0.206^{**}
S3	S4	0.310^{**}	0.000	0.374^{**}	0.000	0.000	0.492^{**}
	S5	0.302^{**}	0.188^{*}	0.220^{**}	0.000	−0.036	0.000
	S6	0.047	0.000	0.432^{**}	0.000	0.000	0.203^{*}
	S7	-0.322^{**}	-0.486^{**}	-0.169^{+}	0.000	0.000	0.000
	S8	0.009	0.740^{**}	-0.428^{**}	0.000	0.000	-0.571^{**}
S4	S5	0.141	0.000	0.486^{**}	0.000	0.000	0.000
	S6	0.073	0.000	0.492^{**}	0.000	0.000	0.207^{**}
	S7	-0.405^{**}	0.000	0.046	-0.588^{**}	0.000	0.000
	S8	−0.100	0.000	-0.458^{**}	-0.500^{**}	0.000	-0.622^{**}
S5	S6	0.089	0.000	0.373^{**}	0.000	0.000	0.000
	S7	−0.146	-0.414^{**}	-0.260^{**}	0.000	0.000	0.000
	S8	0.006	0.755^{**}	-0.323^{**}	0.000	0.000	0.000
S6	S7	-0.209^{+}	0.000	-0.259^{**}	0.000	0.000	0.000
	S8	0.188	0.000	-0.285^{**}	0.000	0.000	-0.420^{**}
S7	S8	0.075	-0.672^{**}	0.067	0.713^{**}	0.000	0.000

*: significant at 0.05 level; **: significant at 0.01 level; +: significant at 0.10 level; r_p : phenotypic correlation coefficient; r_{Ao} : embryo additive correlation coefficient; r_{Do} : embryo dominance correlation coefficient; r_C : cytoplasmic correlation coefficient; r_{Am} : maternal plant additive correlation coefficient; r_{Dm} : maternal plant dominance correlation coefficient.

Table 3 Estimates of conditional correlation coefficients of FSS (fresh seed size) **at eight developmental stages**

Stage 1	Stage 2	r_p	r_{Ao}	r_{Do}	r_C	r_{Am}	r_{Dm}
S1|initial	S2 | S1	−0.122	0.000	0.000	-0.379^{**}	0.000	0.000
	S3 | S2	0.115	0.391^{**}	0.000	0.000	0.000	0.079
	S4 | S3	0.154^{+}	0.000	0.000	0.257^{**}	0.000	0.000
	S5 | S4	−0.028	0.000	0.000	0.000	0.000	−0.093
	S6 | S5	-0.291^{**}	0.000	0.000	-0.459^{**}	0.000	0.000
	S7 | S6	-0.289^{**}	0.000	0.000	-0.411^{**}	0.000	-0.125^{+}
	S8 | S7	0.006	−0.051	0.000	0.000	0.000	-0.156^{*}
S2|S1	S3 | S2	0.083	0.000	0.053	0.000	0.000	0.000
	S4 | S3	−0.111	0.000	0.000	-0.204^{**}	0.000	0.000
	S5 | S4	0.328^{**}	0.000	0.000	0.000	0.000	0.000
	S6 | S5	−0.142	0.000	0.287^{**}	−0.077	0.000	0.000
	S7 | S6	−0.078	0.000	0.049	0.042	0.000	0.000
	S8 | S7	-0.197^{+}	0.000	0.240^{**}	0.000	0.000	0.000
S3|S2	S4 | S3	−0.015	0.000	0.000	0.000	0.039	0.000
	S5 | S4	0.251^{*}	0.000	0.000	0.000	0.478^{**}	0.444^{**}
	S6 | S5	−0.055	0.000	0.124	0.000	0.199^{*}	0.000
	S7 | S6	−0.039	0.000	0.047	0.000	0.000	-0.214^{**}
	S8 | S7	0.128	0.645^{**}	-0.573^{**}	0.000	-0.266^{**}	-0.419^{**}
S4|S3	S5 | S4	−0.090	0.000	0.000	0.000	0.352^{**}	0.000
	S6 | S5	0.038	0.000	0.000	-0.139^{+}	0.325^{**}	0.000
	S7 | S6	-0.207^{**}	0.000	0.000	-0.315^{**}	0.000	0.000
	S8 | S7	0.151	0.000	0.000	0.000	-0.152^{*}	0.000
S5|S4	S6 | S5	0.240^{*}	0.000	0.000	0.000	0.471^{**}	0.000
	S7 | S6	0.130	0.000	0.000	0.000	0.000	0.270^{**}
	S8 | S7	-0.263^{*}	0.000	0.000	0.000	-0.686^{**}	-0.351^{**}
S6|S5	S7 | S6	0.392^{**}	0.000	−0.097	0.570^{**}	0.000	0.000
	S8 | S7	-0.282^{*}	0.000	0.009	0.000	-0.191^{*}	0.000
S7|S6	S8 | S7	−0.123	0.000	-0.153^{+}	0.000	0.000	−0.038

* : significant at $P<0.05$;**: significant at $P<0.01$; +: significant at $P<0.10$; r_p : phenotypic correlation coefficient; r_{Ao} : embryo additive correlation coefficient; r_{Do} : embryo dominance correlation coefficient; r_C : cytoplasmic correlation coefficient; r_{Am} : maternal plant additive correlation coefficient; r_{Dm} : maternal plant dominance correlation coefficient.

$r_{Dm\mathrm{S3/S8}}$ and conditional $r_{Dm(\mathrm{S3|S2})/(\mathrm{S8|S7})}$, that embryo additive effects at S3, embryo dominance effects at S2 and S3, maternal plant dominance effects at S1 and S3 could ultimately affect the performance of FSS through corresponding genetic system. Although it was not significant for unconditional $r_{Do\mathrm{S7/S8}}$, $r_{Am\mathrm{S3/S8}}$, $r_{Am\mathrm{S4/S8}}$, $r_{Am\mathrm{S5/S8}}$, $r_{Am\mathrm{S6/S8}}$, $r_{Dm\mathrm{S5/S8}}$, conditional $r_{Do(\mathrm{S7|S6})/(\mathrm{S8|S7})}$, $r_{Am(\mathrm{S3|S2})/(\mathrm{S8|S7})}$, $r_{Am(\mathrm{S4|S3})/(\mathrm{S8|S7})}$, $r_{Am(\mathrm{S5|S4})/(\mathrm{S8|S7})}$, $r_{Am(S6|S5)/S8|S7}$, $r_{Am(\mathrm{S5|S4})/(\mathrm{S8|S7})}$ were significant, which showed that net embryo dominance effect at S7, net maternal plant additive effects at S3–S6, net maternal plant dominance at S5 could influence intimately the mature FSS by corresponding genetic system.

2. 3. 2 DSS

Estimation of unconditional and conditional genetic correlation coefficients of DSS with itself at various intervals is summarized in Tables 4 and 5, respectively. Insignificantly unconditional phenotypic correlation coefficient indicated that accumulated gene effects would not influence on mature DSS except S7. While conditional $r_{p(\mathrm{S1|initial})/(\mathrm{S8|S7})}$, $r_{p(\mathrm{S2|S1})/(\mathrm{S8|S7})}$, $r_{p(\mathrm{S3|S2})/(\mathrm{S8|S7})}$, $r_{p(\mathrm{S4|S3})/(\mathrm{S8|S7})}$, $r_{p(\mathrm{S5|S4})/(\mathrm{S8|S7})}$, $r_{p(\mathrm{S6|S7})/(\mathrm{S8|S7})}$, $r_{p(\mathrm{S7|S8})/(\mathrm{S8|S7})}$ were significant at 0.10, 0.05, or 0.01 levels, suggesting that net gene effects expressed at various periods would affect the final performance of DSS. Similarly, genetic effects due to embryo, cytoplasm, and maternal plant system could influence the relationships of various stages to mature solely or simultaneously. It was shown by significant $r_{Ao\mathrm{S1/S8}}$ and $r_{Ao(\mathrm{S1|initial})/(\mathrm{S8|S7})}$, $r_{Ao\mathrm{S7/S8}}$ and $r_{Ao(\mathrm{S7|S6})/(\mathrm{S8|S7})}$, $r_{C\mathrm{S2/S8}}$ and $r_{C(\mathrm{S2|S1})/(\mathrm{S8|S7})}$, $r_{Dm\mathrm{S1/S8}}$ and $r_{Dm(\mathrm{S1|initial})/(\mathrm{S8|S7})}$ that embryo additive effects at S1 and S7, cytoplasm effects at S2, maternal plant dominance effects at S1 could ultimately affect the performance of DSS.

Table 4 Estimates of unconditional correlation coefficients of DSS (dry seed size) **at eight developmental stages**

Stage 1	Stage 2	r_p	r_{Ao}	r_{Do}	r_C	r_{Am}	r_{Dm}
S1	S2	0.246^{*}	0.244^{**}	0.000	0.177^{*}	0.000	-0.405^{**}
	S3	0.152	0.229^{**}	0.000	−0.068	0.301^{**}	0.248^{**}
	S4	0.226^{*}	0.000	0.000	0.095	0.000	0.043
	S5	0.187^{+}	0.000	0.000	0.066	0.669^{**}	-0.838^{**}
	S6	0.251^{*}	0.000	0.000	0.000	0.000	−0.127
	S7	-0.216^{*}	-0.256^{**}	0.000	0.000	0.620^{**}	-1.000^{**}
	S8	0.121	0.319^{**}	0.000	0.056	0.000	-1.000^{**}
S2	S3	0.246^{*}	0.192^{*}	0.000	0.752^{**}	0.000	0.006
	S4	0.282^{*}	0.000	0.063	0.920^{**}	0.000	−0.044
	S5	0.230^{*}	0.000	−0.004	0.709^{**}	0.000	-0.284^{**}
	S6	0.198	0.000	0.298^{**}	0.000	0.000	-0.211^{**}
	S7	−0.159	-0.325^{**}	0.000	0.000	0.000	-0.434^{**}
	S8	−0.020	0.371^{**}	0.033	-0.728^{**}	0.000	-0.420^{**}
S3	S4	0.292^{**}	0.000	0.000	0.355^{**}	0.000	0.480^{**}
	S5	0.222^{+}	0.000	0.000	0.094	0.092	0.380^{**}
	S6	0.229^{+}	0.000	0.000	0.000	0.000	0.410^{**}
	S7	−0.079	-0.447^{**}	0.000	0.000	0.145^{+}	0.034
	S8	−0.017	0.581^{**}	0.000	-0.535^{**}	0.000	-0.508^{**}
S4	S5	0.094	0.000	0.644^{**}	−0.027	0.000	0.308^{**}
	S6	0.156	0.000	0.582^{**}	0.000	0.000	0.378^{**}
	S7	−0.160	0.000	0.000	0.000	0.000	−0.032
	S8	−0.067	0.000	−0.009	-0.385^{**}	0.000	-1.000^{**}
S5	S6	0.060	0.000	0.521^{**}	0.000	0.000	0.331^{**}
	S7	−0.159	0.000	0.000	0.000	0.857^{**}	−0.081
	S8	0.018	0.000	0.009	−0.022	0.000	-0.745^{**}
S6	S7	-0.205^{+}	0.000	0.000	0.000	0.000	0.142^{+}
	S8	−0.031	0.000	−0.002	0.000	0.000	-0.659^{**}
S7	S8	-0.227^{*}	-0.516^{**}	0.000	0.000	0.000	-1.000^{**}

*:Significant at $P<0.05$; **: significant at $P<0.01$; +: significant at $P<0.10$; r_p : phenotypic correlation coefficient; r_{Ao} : embryo additive correlation coefficient; r_{Do} : embryo dominance correlation coefficient; r_C : cytoplasmic correlation coefficient; r_{Am} : maternal plant additive correlation coefficient; r_{Dm} : maternal plant dominance correlation coefficient.

Table 5 Estimates of conditional correlation coefficients of DSS (dry seed size) at eight developmental stages

Stage 1	Stage 2	r_p	r_{Ao}	r_{Do}	r_C	r_{Am}	r_{Dm}
S1|initial	S2|S1	−0.160	0.000	0.000	-0.528^{**}	0.000	0.000
	S3|S2	0.039	0.113	0.000	0.000	0.269^{**}	0.682^{**}
	S4|S3	0.061	0.000	0.000	0.000	0.235^{**}	0.000
	S5|S4	0.080	0.046	0.000	0.240^{*}	0.049	0.000
	S6|S5	0.174^{+}	0.000	0.000	0.270^{**}	0.216^{*}	-0.300^{**}
	S7|S6	-0.323^{**}	-0.356^{**}	0.000	-0.628^{**}	0.000	-1.000^{**}
	S8|S7	-0.338^{**}	-0.514^{**}	0.000	-0.412^{**}	0.000	-0.880^{**}
S2|S1	S3|S2	0.147	0.000	0.000	0.000	0.000	0.000
	S4|S3	0.144^{+}	0.000	−0.075	0.000	0.000	0.000
	S5|S4	0.015	0.000	0.000	-0.370^{**}	0.000	0.000
	S6|S5	−0.116	0.000	0.186^{**}	-0.140^{*}	0.000	0.000
	S7|S6	0.078	0.000	0.000	0.697^{**}	0.000	0.000
	S8|S7	0.344^{**}	0.000	0.000	1.000^{**}	0.000	0.000
S3|S2	S4|S3	0.032	0.000	0.000	0.000	0.036	0.000
	S5|S4	−0.119	-0.269^{**}	0.000	0.000	-0.250^{**}	0.000
	S6|S5	0.186^{+}	0.000	0.000	0.000	0.191^{+}	0.313^{**}
	S7|S6	0.002	-0.173^{+}	0.000	0.000	0.000	0.049
	S8|S7	0.174^{+}	−0.014	0.000	0.000	0.000	0.254^{**}
S4|S3	S5|S4	−0.147	0.000	0.000	0.000	0.125	0.000
	S6|S5	−0.067	0.000	−0.006	0.000	0.143	0.000
	S7|S6	−0.093	0.000	0.000	0.000	0.000	0.000
	S8|S7	0.194^{+}	0.000	0.000	0.000	0.000	0.000
S5|S4	S6|S5	0.020	0.000	0.000	−0.078	0.244^{*}	0.000
	S7|S6	-0.208^{*}	-0.221^{**}	0.000	-0.480^{**}	0.000	0.000
	S8|S7	-0.358^{**}	-0.243^{**}	0.000	-0.556^{**}	0.000	0.000
S6|S5	S7|S6	-0.146^{+}	0.000	0.000	-0.202^{*}	0.000	-0.163^{+}
	S8|S7	-0.203^{**}	0.000	0.000	-0.427^{**}	0.000	0.089
S7|S6	S8|S7	0.451^{**}	0.429^{**}	0.000	0.817^{**}	0.000	−0.015

*: significant at $P<0.05$; **: significant at $P<0.01$; + : significant at $P<0.10$; r_p : phenotypic correlation coefficient; r_{Ao} : embryo additive correlation coefficient; r_{Do} : embryo dominance correlation coefficient; r_C : cytoplasmic correlation coefficient; r_{Am} : maternal plant additive correlation coefficient; r_{Dm} : maternal plant dominance correlation coefficient.

3 Discussion

There were expression, regulation, and interaction of polygene that controlled the final performance of soybean seed size. The genetic effects estimated from the ultimate phenotypic value reflected the integrated role of polygene at different growth stages and could not make clear the expression, regulation, and interaction of polygene. To understand the developmental genetic law of seed size and to find theory for yield improvement in soybean, it is necessary to research the effect of difference of gene expression on dynamic of seed size.

Zhu *et al.* [11-14] proposed a new seed model to unbiased estimate the variances and covariance due to seed model by only using several generation means.

Total phenotypic variance (V_P) is composed of variance components of genotypic and residual effects ($V_P = V_G + V_e$). Among genotypic variance ($V_G = V_o + V_C + V_M$), variance of embryo effects ($V_o = V_{Ao} + V_{Do}$) measures genetic variation contributed by the embryo gene effects (embryo additive effect V_{Ao}, embryo dominance effect V_{Do}), variance of cytoplasm effect (V_C) and maternal nuclear effects ($V_m = V_{Am} + V_{Dm}$) reveals the contribution of maternal plant through effects of cytoplasm and maternal nuclear genes. Furthermore, Zhu[20] developed a mixed model approach by combining the seed model with conditional analysis approach, and variance of net genetic effects at different periods and correlation between them could be obtained for the quantitative traits during the development. There were different concepts between unconditional and conditional variation. Unconditional variation represents the accumulated genetic variation from initial time to time *t*, while conditional variation refer to as net genetic variation from time *t*-1 to *t*. Since seed development is a dynamic process, gene expression should not always be the same as for developmental quantitative traits. For instance, unconditional embryo additive variance was significant at S2, S5, and S7, while conditional embryo additive variance showed that the net genetic effect was zero at these stages for FSS. Furthermore, analysis unconditional maternal plant additive variance indicated that there was no gene action at S4, S6, and S8, but conditional variances such as $V_{Am(\mathrm{S4|S3})}$, $V_{Am(\mathrm{S6|S5})}$, $V_{Am(\mathrm{S8|S7})}$ were detected. Thus, conditional analysis contributes to comprehension of the expression and action of genes during developmental process of seed. By the combination of unconditional and conditional methods, dynamic consequence of genetic effects could be revealed for different developmental traits at specific periods. For example, there were actually no new effects of gene expression in the second period, but significant unconditional maternal dominance variances of fresh and dry weight were detected due to accumulated results of early stages. Although no significant unconditional cytoplasm effects for dry weight were detected at S6 and S7, there were net genetic effects of cytoplasm from S6 to S7, which might not be large enough to be detected by the unconditional method. Therefore, the conditional analysis method could help to have a glimpse of the genetic effects of new gene expression before being detected by unconditional method.

Different growth stages may affect the ultimate performance of seed size. By correlation analysis, it was showed that net embryo dominance effect at S7, net maternal plant additive effects at S3-S6, net maternal plant dominance at S5 could influence intimately the mature FSS, and embryo additive effect at S1 and S7, cytoplasm effects at S2, maternal plant dominance effects at S1 could ultimately affect the performance of seed size. The possible reason for difference of gene effects at different stages might be that ploygene system of quantitative traits had specific expression pattern at different developmental periods, which might be controlled by different loci of the ploygene system. For instance, Wu *et al.*[30] reported that different QTLs could modify the growth of the *Populus*.

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大豆籽粒大小的发育遗传分析

李文霞 [1,2,3]，宁海龙 [1,3]，李文滨 [1,3]，吕文河 [2]

1. 东北农业大学大豆研究所，哈尔滨 150030；
2. 东北农业大学农学院，哈尔滨 150030
3. 教育部大豆生物学重点实验室，哈尔滨 150030

摘 要：籽粒大小是大豆产量的一个重要因素。有关大豆籽粒的遗传学和生理生态学研究已有一些研究, 而对于籽粒发育过程中的遗传效应却报道很少。文章采用种子广义遗传模型, 分析了大豆双列杂交组合 3 个世代遗传材料 8 个时期的鲜籽粒大小和干籽粒大小的数据, 应用非条件和条件遗传方差及相关方法分析了发育遗传规律。8 个时期的亲本、F_1、F_2 的鲜籽粒大小和干籽粒大小的平均数分别在 9/6 和 9/13 达到最高值, 鲜籽粒大小在 9/6 后迅速下降, 干籽粒大小在 9/13 后区于稳定。非条件方差分析表明在整个生育期中, 胚遗传效应、细胞质遗传效应和母体植株遗传效应对大豆鲜籽粒大小和干籽粒大小有影响。在多数生育阶段中, 细胞质和母体植株的遗传效应对鲜籽粒大小和干籽粒大小影响较大。条件方差分析表明, 在大豆生育期中, 各遗传体系的基因间断性表达。在多数生育阶段中, 细胞质和母体植株的净遗传效应高于胚净遗传效应。不同时期的各遗传体系的基因效应可以单独或同时影响鲜籽粒大小和干籽粒大小的最终表现。8/16 的胚加性效应、8/9 和 8/16 的胚显性效应、8/2 和 8/16 的母体植株显性效应影响到鲜籽粒大小的最终表现。8/2 和 9/13 的胚加性效应、8/9 的细胞质效应、8/2 的母体植株显性效应对干籽粒大小的最终表现有影响。

关键词：发育；遗传效应；鲜籽粒大小；干籽粒大小；大豆

作者简介：李文霞（1974-），女，黑龙江省双鸭山市人，博士研究生，专业方向：作物遗传育种与生物技术